

Wind dispersal results in a gradient of dispersal limitation and environmental match among discrete aquatic habitats

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Directional dispersal by wind and other dispersal agents may generate spatial patterns in passively dispersing metacommunities which cannot be detected by classical eigenvector methods based on Euclidean distances. We analysed zooplankton communities (Rotifera, Cladocera, Copepoda) in a cluster of soda pans distributed over a short spatial scale of 18 km and tested explicitly for directional signals in their spatial configuration. The study area is exposed to a prevailing northwestern wind direction. By applying asymmetric eigenvector maps (AEM), we were able to identify corresponding directionality in the spatial structure of communities. Furthermore, the match between community composition and environmental conditions exhibited a spatial pattern consistent with the prevailing wind corridor, with best match found downwind the dominant wind direction. We also found that classical eigenvector methods based on Euclidean distances underestimated the role of spatial processes in our data. Our study furthermore shows that dispersal limitation may constrain community assembly in highly mobile organisms even at spatial scales below 5 km.

Spatial processes are increasingly recognized as important factors underlying local community assembly and regulation of diversity (Borcard et al. 1992, Leibold et al. 2004, Legendre and Gauthier 2014). Dispersal limitation is a fundamental aspect of biogeographic patterns and its implications for macroorganisms is generally well acknowledged (Martiny et al. 2006). Recent analyses revealed that, in contrast to the long-standing tenet ‘everything is everywhere’, even communities of microscopic organisms may be subject to dispersal limitation (Vyverman et al. 2007, Fontaneto et al. 2008, Ptacnik et al. 2008, 2010, Barton et al. 2010, Soininen et al. 2012). According to the emerging paradigm, spatial patterns in regional diversity resulting from dispersal limitation are indeed rather general phenomena. The metacommunity concept provides a general framework to understand the relative role of both spatial and local driving forces of community patterns and hence the relative importance of dispersal limitation in diversity maintenance (Leibold et al. 2004).

Various distance decay analyses support the general importance of spatial processes (Soininen et al. 2007, Shurin et al. 2009, Martiny et al. 2011, Astorga et al. 2012). While there is some agreement on the relevance of dispersal limitation for microscopic organisms across larger spatial scales (> 100 km), the ecological implications of such spatial patterns at smaller scales are less clear. Dispersal rates depend on the degree of connectivity among individual habitats. High dispersal rates may override local environmental selection, resulting in mass effects (Mouquet and Loreau

2003, Leibold et al. 2004, Heino et al. 2015). Conversely, strong dispersal limitation prevents potential colonizers from reaching suitable patches, which leaves local ecological niches vacant. An ideal match between local environment and species composition is therefore expected at intermediate dispersal rates, where the role of mass effects and the lack of colonisers are both minimized (Fig. 1; Declerck et al. 2013).

In order to test whether spatial patterns in ecological data are influenced by dispersal limitation, the degree of connectivity among habitats must be parameterised appropriately (Moritz et al. 2013). To date, most metacommunity studies dealing with distinct habitats approximate connectivity by Euclidean distance among habitats. This approach assumes omnidirectional dispersal of propagules. However, in reality, it may be an exception and dispersal is biased in selected directions (Vuilleumier and Possingham 2006).

For discrete, unconnected habitat patches, wind is one of the most important agents of passive dispersal, along with possible animal (waterbirds, amphibians, mammals) or human vectors (Maguire 1963, Bilton et al. 2001, Havel and Shurin 2004). Wind direction can be a major factor for pollination or seed dispersal (Bullock and Clarke 2000), although directionality is frequently ignored in the study of anemochory (Levin et al. 2003). Similarly, its explicit spatial representation is generally missing from metacommunity studies (Moritz et al. 2013), even though there is empirical evidence for the effect of wind on the amount of dispersed propagules (Vanschoenwinkel et al. 2008, 2009).

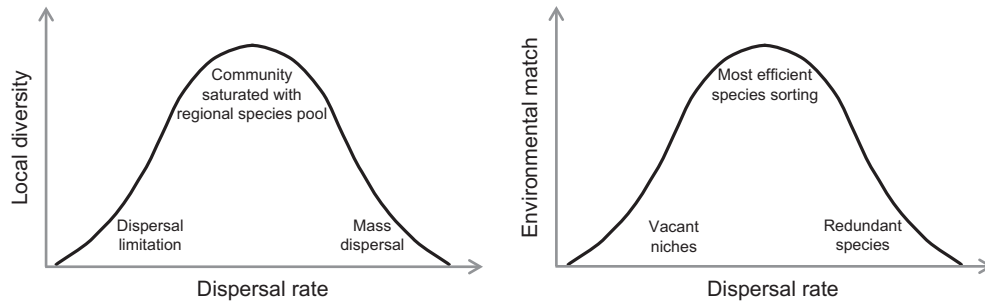


Figure 1. Effect of dispersal rate on local species richness (left; after Mouquet and Loreau 2003) and the role of dispersal rate in generating environmental match in metacommunities (right; after Declerck et al. 2013).

Spatial eigenfunction analyses are modern tools to explore spatial patterns in metacommunities (Legendre and Legendre 2012). The construction of principal coordinates of neighbour matrices (PCNM) is based on Euclidean (geographic) distances among sampling sites (Borcard and Legendre 2002). The Moran's eigenvector maps (MEM) method, a generalisation of PCNM, enables the usage of different types of spatial weights and connection diagrams (Dray et al. 2006) and is useful to describe connectivity in dendritic networks and fluvial systems. The recently introduced asymmetric eigenvector maps (AEM) allow an explicit representation of directionality in spatial data (Blanchet et al. 2008). So far, AEM was successfully applied to fluvial networks, including rivers, fluvial lakes and coastal systems with prevailing currents (Blanchet et al. 2011, Sharma et al. 2011, Bertolo et al. 2012, Liu et al. 2013, Padial et al. 2014).

We provide here the first test for directionality in a metacommunity consisting of distinct habitats. We perform our analysis on the zooplankton communities of soda pans in the Seewinkel region, on the bordering lowland area between eastern Austria and western Hungary. These habitats are shallow saline ponds and lakes holding sodic water, located in an area with a prevailing northwestern wind direction. Being temporary habitats, their zooplankton communities depend on the production of a resting egg bank. Soda pans typically fall dry in late summer when the resting egg bank gets exposed to wind. We combine our analysis with a test on the ecological (mis)match between local environment and community composition in order to distinguish spatial pattern caused by dispersal limitation from those caused by mass effects.

Materials and methods

Study area and sample collection

Seewinkel is part of a UNESCO World Heritage Site. Due to the topography of the surrounding areas, the region experiences very constant northwestern winds. In fact, on a continental scale, this northwestern part of the lowlands of the Carpathian Basin is situated in a 'wind tunnel' between the eastern mountains of the Alps and the westernmost parts of the Carpathian Mountains. Seewinkel has sodic soil and several extremely shallow (< 1 m) intermittent saline aquatic habitats, so-called soda pans were formed in a relatively small confined region (approx. 200 km², with a min. distance of

0.1 km and a max. of 18 km among pans; Boros et al. 2014). They have surface areas ranging from 0.2 to 97.3 ha and are spatially discrete ecosystems without natural in- or outflow. They are mainly fed by groundwater upwellings, with the additional source of precipitation (Boros et al. 2013, 2014).

We sampled 34 astatic soda pans of Seewinkel (Fig. 2) during the early summer of 2009 or 2010 (between 9 and 11 June 2009 or on 2 June 2010). When water depth was too low for a representative sample in 2009 (or a pan has already dried out), sampling was repeated in the same period of 2010, and only the latter data were used in the analyses. Details on the sampling campaign, local environmental parameters and a zooplankton species list are reported by the authors in former studies (Boros et al. 2014, Horváth et al. 2014, Tóth et al. 2014). We measured water depth, Secchi disk transparency, pH, conductivity, total suspended solids (TSS), chlorophyll-a (chl) and total phosphorus (TP) as major local environmental variables. For each pan, we also determined the total area (area of lakebed, km²), along with the proportion of open water (non-vegetated) area (%), and recorded exact GPS locations (centre of each pan). Details on the measurements are presented in former studies by the authors (Horváth et al. 2013, 2014).

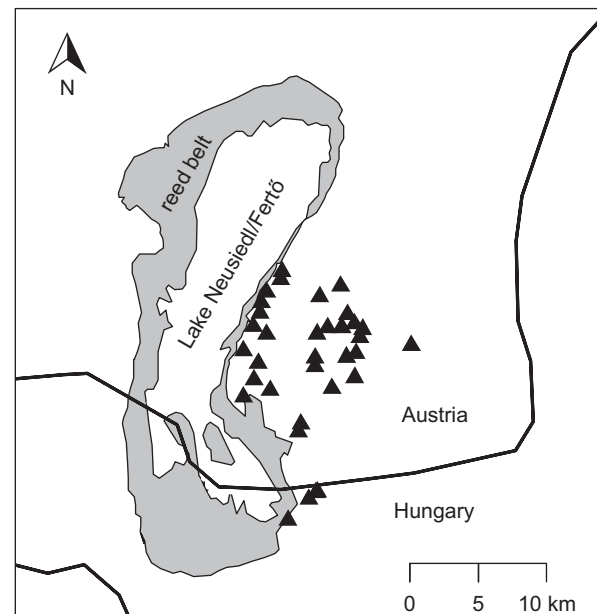


Figure 2. Map with the location of the investigated 34 pans (triangles) in the Seewinkel region.

Data analysis

We used presence–absence data of zooplankton species (Rotifera, Cladocera, Copepoda) in all analyses. Among local environmental predictors, water depth, Secchi disk transparency, conductivity, TSS, TP, chl and surface area were all ln-transformed to normalise their distribution. There was a rather high number of rare species (44 out of 75) with only one or two habitats of occurrence. Very rare taxa add over-proportionally to the stochasticity in community data, as they do not provide a good basis for similarity measurements among sites. Moreover, species with single or very few observations provide only stochastic information about the environmental niche of a given species. We therefore excluded these rare species from all analyses. Excluding rare species generally enhanced the fit of our empirical models in terms of total explained variation, but the results are qualitatively in agreement with the results obtained with the full dataset (Supplementary material Appendix 2).

We selected the most relevant local predictors from all available local environmental parameters by means of a redundancy analysis (RDA) on the zooplankton community. We used forward selection (permutation test with 999 permutations) to only retain significant ($p < 0.05$) variables. Those were Secchi disk transparency, conductivity and TSS, which were grouped as ‘local variables’ for later analyses. In order to safeguard against any bias arising from the forward selection method, we repeated the analysis employing two alternative methods for model selection (removal of collinear predictors and retaining all predictors). The results were consistent with all methods (Supplementary material Appendix 2).

Wind dispersal of zooplankton resting stages is assumed to be effective especially over shorter distances (Brendonck and Riddoch 1999, Caceres and Soluk 2002, Cohen and Shurin 2003, Vanschoenwinkel et al. 2009). To test this assumption, we split the distances between habitats into four classes (0–5, 5–10, 10–15 and above 15 km) and compared the importance of directionality among these distance classes (Fig. 3). As we found that AEM indeed had the highest power below 10 km, we used this truncation distance in our AEM and MEM models.

We tested for the potential role of directional connectivity by comparing two eigenvector methods that are

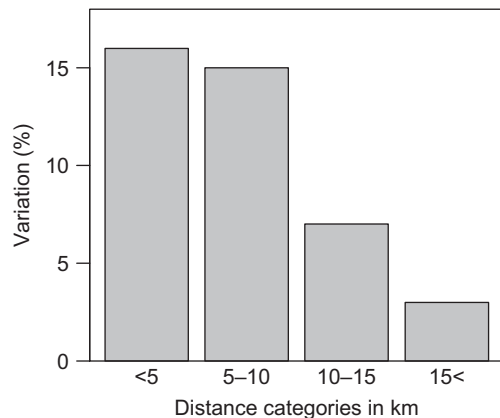


Figure 3. Pure directional spatial component of total community variation (%) in the variation partitioning model of AEM for four different distance categories.

based on Euclidean distance (PCNM and MEM) with the AEM method, which calculates eigenvectors according to a pre-defined connectivity-angle. To compare the results from MEM and AEM, we tested for a difference in their explanatory power based on a connection diagram with a truncation distance of 10 km. Also, we compared the variation explained by AEM and MEM with results from a basic PCNM (with no distinct truncation threshold). We first computed spatial eigenfunctions of MEM and AEM. When comparing results of AEM and MEM, we always used the same connection diagram of habitats (see below), while for the AEM method, directionality was applied according to the prevailing wind direction during summer, when the pans generally dry out and their egg banks get exposed to wind. Western-northwestern wind (292.5°) dominates during this period (WindFinder.com GmbH & Co. KG 2014) and eigenvectors were hence computed for this wind direction. To select significant spatial vectors, we ran the same forward selection procedure as outlined above for local predictors on all positive MEM and AEM eigenvectors, with the community matrix as the dependent variables. With significant local and spatial variables, we finally ran variation partitioning (Borcard et al. 1992). For all positive PCNM eigenvectors, we first ran forward selection, and then performed variation partitioning on the two groups of variables.

In order to test the role of prevailing wind direction over incidental directional similarity, we compiled a radiogram based on the variation explained by AEM in 16 different wind directions. Here we again used 10 km as the truncation distance, similar to the previous AEM and MEM analyses outlined above. The selection procedure of AEM eigenvectors and afterwards the variation partitioning was also the same. We calculated the pure spatial effect (based on AEM) in all 16 directions and compared our results with the distribution of wind directions in the region.

For studying the role of wind in generating or elucidating environmental mismatch at the local sites (i.e. the disagreement between local species composition and environment), we first built a principal component analysis (PCA) model for the local predictors significantly affecting community composition. The first PCA axis was then fed into an RDA and a canonical correspondence analysis (CCA) on community data. As the CCA model ($R^2 = 0.74$) gave a better fit over RDA ($R^2 = 0.62$), we used the CCA for further analysis. We quantified environmental mismatch as the unexplained variation of this CCA, i.e. the absolute sum of site scores of all unconstrained axes, weighted by the importance of each axes. The spatial pattern of this residual variation was analysed as a smooth spatial grid, using a generalized additive model (GAM). The R script used for calculating mismatch is provided in Supplementary material Appendix 3. Significant spatial eigenvectors for all analyses are given in Supplementary material Appendix 4, Table A1 and A2.

We used the ‘vegan’ package in R (Oksanen et al. 2012, R Development Core Team) for running RDA, CCA, PCA, PCNM and variation partitioning, ‘packfor’ (Dray 2013) for forward selection, ‘spacemaker’ (Dray 2008) for MEM, ‘AEM’ (Blanchet 2010) for AEM, and ‘mgcv’ (Wood 2011) for generalized additive models (GAM).

Table 1. Variation partitioning based on significant local environmental variables and eigenvectors of PCNM, MEM and AEM as the spatial components. Values are given in %. Pure fractions larger than zero are significant in all cases ($p < 0.05$).

	Pure environmental	Shared	Pure spatial	Unexplained
PCNM	14	4	5	77
MEM	18	0	0	82
AEM	9	9	13	69

Results

In the first variation partitioning analysis, space was represented by PCNM eigenvectors which were calculated from the Euclidean distance matrix among sampling sites. This analysis revealed a weak but significant effect for space (5%), while local environment explained a much higher fraction (14%). Next, MEM eigenvectors were calculated applying a truncation distance of 10 km, again based on Euclidean space. None of the MEM eigenvectors was significant; hence no pure spatial effect could be detected. Once directionality was considered in the AEM model in addition to the same truncation distance (10 km), the proportion of both the total explained variation (from 18 to 31%) and the pure spatial component (from 0 to 13%) increased clearly compared to the MEM approach (Table 1). We then tested whether the spatial component was indeed related to the actual wind direction, by calculating a radiogram across all wind directions. The direction with highest explained variation in fact coincided with the actual wind direction in the area, further validating the effect of directionality (Fig. 4).

In order to test how the spatial effect was related to community assembly, we calculated the match of community composition and environment for each site and calculated a spatial grid of this ecological (mis)match. The analysis revealed that mismatch peaked at the upwind (northwestern) side and was also high at peripheral regions parallel to the wind corridor, while match was higher in the centre of the area and the downwind (southeastern) part of the corridor (Fig. 4).

Discussion

Directional similarity can be prominent in metacommunities of fluvial networks (Blanchet et al. 2011, Sharma et al. 2011, Bertolo et al. 2012, Liu et al. 2013, Padial et al. 2014), but has not been considered among discrete waterbodies before. Our study provides the first evidence for directional similarity in communities of distinct systems that are not physically connected. The effect of wind as a driver of metacommunity patterns was attributable to its role in lessening dispersal limitation along its prevailing direction, which was evidenced from the decreasing environmental mismatch along this axis.

We have shown previously that salinity is generally outstanding as a local environmental parameter structuring zooplankton communities in soda pans (Horváth et al. 2014). In the Seewinkel area, salinity shows a longitudinal gradient, with a more continuous salt-rich soil layer in the west (Metz and Forró 1991). As the prevailing spatial similarity in salinity (measured as conductivity) is rather

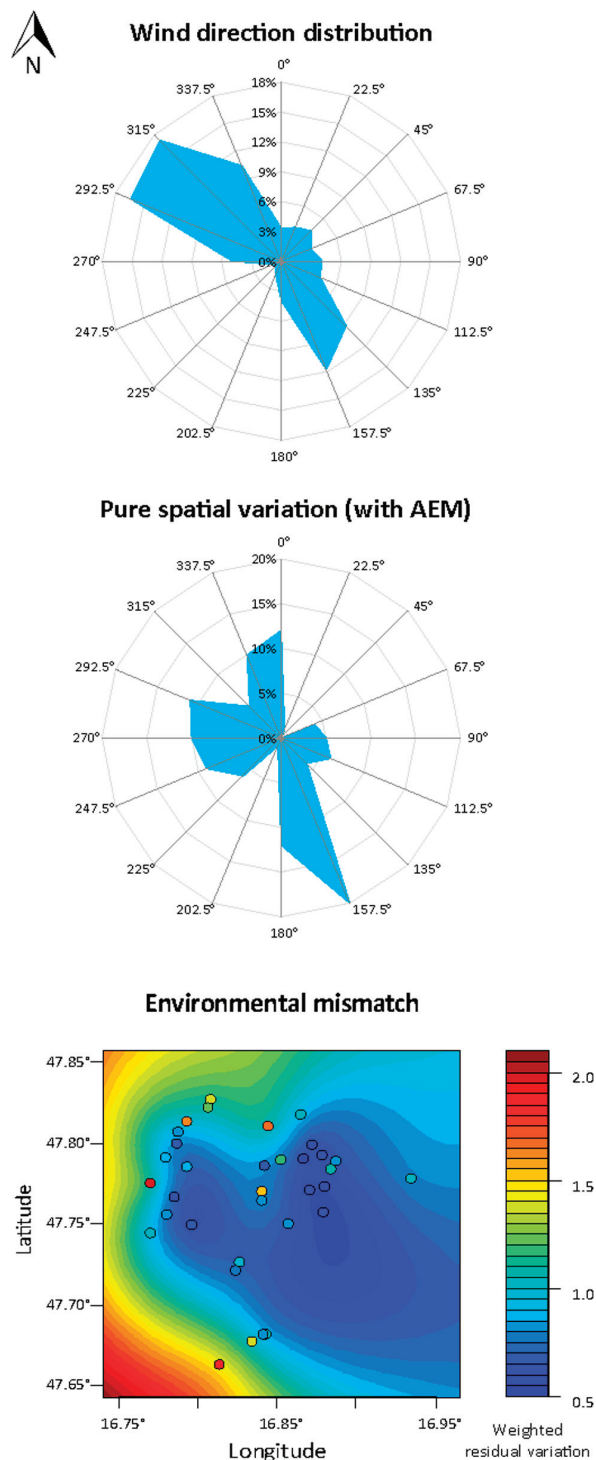


Figure 4. Radar charts representing the annual wind direction distribution in the area in % (above), the variation explained by AEM as the pure spatial component in respective angles of the directional component (middle) and the mismatch between community data and local environment, projected for the region (below). The colour bar on the right side of the mismatch plot illustrates colour coding for the mismatch values, which were calculated as the unexplained variation of a CCA, i.e. the absolute sum of site scores of all unconstrained axes, weighted by the importance of each axes (see more details in Material and methods and Supplementary material Appendix 3). Points illustrate the original values, while the background shows the values predicted by a generalised additive model (GAM).

orthogonal to the prevailing wind direction, our findings cannot be explained by a correlation with salinity. In line with this, the pure spatial effect of AEM explained more of the total community variation than conductivity together with three other local variables (water depth, Secchi disk transparency, TSS; Table 1).

In soda pans, dispersal should especially happen during summer and early autumn, when the pans usually fall dry, exposing the egg bank to wind. During this dry phase, soda dust blown by wind is a conspicuous phenomenon, clearly visible due to the white colour of the sediment. In fact, exposure and consequent wind dispersal of crustacean zooplankton was shown to play a prominent role in the colonisation of small temporary waterbodies like rock pools (Altermatt et al. 2008, Altermatt and Ebert 2010).

In permanent waterbodies, however, directionality may be more difficult to identify, yet may be equally important. Especially waterfowl and ephemeral insects are efficient dispersal vectors in such systems (Bilton et al. 2001). As these active flyers are selective in their choice of habitats and may exhibit directional migration (like the seasonal migration of waterbirds), directionality may also emerge at much larger spatial scales (Figuerola et al. 2005, Muñoz et al. 2013).

Along the main wind direction, our results are in good agreement with former studies that showed that wind is a highly effective dispersal agent especially within small spatial scales (Caceres and Soluk 2002, Cohen and Shurin 2003, Vanschoenwinkel et al. 2009). This is supported by the decreasing effect of directional wind dispersal after 10 km (Fig. 3) and the overall higher environmental match in central habitats (see the slightly increasing mismatch in the gap after the first clutch of habitats in Fig. 4).

The better match between community composition and environment seen in the central and downwind sites implies that even the best connected sites did not exhibit mass effects. Our dispersal gradient therefore is situated left to the hump seen in Fig. 1 (from dispersal limitation to saturated communities). The results thereby disagree with other studies which found no dispersal limitation in zooplankton over very short scales (< 1 km; Vanschoenwinkel et al. 2007) or within distances comparable to our study scale (< 10 km; Cottenie et al. 2003, Declerck et al. 2011). These latter studies, however, targeted permanent systems. Our results hence support the idea that temporary waterbodies can especially be prone to dispersal limitation (Heino et al. 2015). This may be linked to the regular 'extinction' of their active communities, which may make these systems particularly dependent on propagule densities. Furthermore, wind can eliminate a substantial share of the dormant egg bank, thus generating higher extinction rates and at the same time, increasing the dependence of local communities on dispersal.

Apart from dispersal limitation per se, our habitat complex furthermore provides an example for dispersal bias due to the dominant wind. While dispersal limitation is generally attributed to the stochastic nature of dispersal (Chase 2010), in our case, wind provides a deterministic dispersal route, biasing the purely distance-based process in a selected direction.

Currently, the standard approach for analysing spatial patterns in non-connected habitats is to assume dispersal

without any directional element, analysed with MEM or PCNM methods (De Bie et al. 2012, Frisch et al. 2012, Florencio et al. 2014, Székely and Langenheder 2014). Our results show, however, that this approach has its limitations. Where information regarding the potential directionality of dispersal agents is available, AEM approach allows for a better representation of spatial patterns and their directional component. For cases where no a priori knowledge or presumption is available on the distance decay of dispersal, the standard PCNM approach (without a distinct truncation threshold) is still a valid method, as its results may also resemble incidental directionality (Supplementary material Appendix 1, Fig. A1). In general, the inspection of the main similarity axes based on MEM or PCNM may help identifying directionality in the data. However, both PCNM and MEM underestimated the role of spatial processes (Table 1). Our results highlight that a proper representation of dispersal routes is mandatory for disentangling the relative role of niche-based vs. neutral processes shaping metacommunities (Heino et al. 2015).

It is very likely that many lentic systems, including pools, ponds and lakes, are affected by strong wind dispersal, especially those of temporary nature. Therefore, exploring the possible directional similarities in such habitat complexes with the help of asymmetric methods like AEM could significantly contribute to our understanding of spatial patterns in metacommunities. Actively dispersing aquatic insects e.g. chironomids may also show directional patterns if the effect of strong winds outweighs their weak flying abilities (Armitage et al. 1995). Additionally, the asymmetric approach would also be useful for those terrestrial systems, where directional dispersal can occur owing to the directional component of agents (wind, animals, pollinators) or the structure of terrestrial elements (e.g. landscape permeability, elevations, forests, hedges).

Conclusions

A frequent claim in the debate on the relative role of spatial factors (dispersal) vs the role of local environment (species sorting) is that spatial effects are easily overrated due to a poor representation of the local environment, especially when there is a local variable (like some climatic factor) that itself exhibits a spatial pattern (Cottenie 2005, Caruso et al. 2011, Martiny et al. 2011). Our analysis shows that the opposite may also be true. Without a proper representation of the spatial structure underlying the connectivity (wind direction), we would have strongly underestimated the spatial signal in our data.

By showing that the match between community composition and environment scales with geographic position along the upwind-downwind gradient, our results moreover illustrate that the dispersal gradient evident in this confined area likely has direct ecological implications for community functioning. In these protected waterbodies, this has crucial implications for connectivity conservation.

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Supplementary material (Appendix ECOG-01685 at <www.ecography.org/appendix/ecog-01685>). Appendix 1–4.